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THE LATE TRIASSIC CANJILON QUARRY (UPPER CHINLE GROUP, NEW MEXICO) PHYTOSAUR SKULLS: EVIDENCE OF SEXUAL DIMORPHISM IN PHYTOSAURS

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Abstract—The Canjilon quarry, located in north-central New Mexico near Ghost Ranch, is a death assemblage of phytosaurs stratigraphically high in the Petrified Forest Formation of the Chinle Group (Revueltian = early-mid Norian). The site yields numerous fossils of *Pseudopalatus*-grade phytosaurs, with at least 11 skulls collected from the locality by Charles Camp in 1928 and 1933 and another one more recently by Ghost Ranch. A re-examination of these skulls reveals two morphotypes that differ only in the lengths and relative robustness of their premaxillae and septomaxillae. In these two morphotypes, the premaxillae define the shape and length of the rostral crest, the dimensions of which are independent of skull size. In one morphotype, the premaxillae are long, thin bones that lead to an abrupt, volcano-like narial crest. In the second morphotype, the premaxillae are of nearly the same length, but expand dorso-ventrally halfway along their lengths, creating a longer and more robust crest. The most parsimonious explanation of these two variants in rostral crest morphology in a single death assemblage is that *Pseudopalatus*-grade phytosaurs were sexually dimorphic. Thus, the larger, more robust crest of the first morphotype is a display feature, most likely of the male animal. The more gracile snout and crest characterize the female morph. In the sample of phytosaurs examined, there are three individuals of the more robust morphotype, six individuals that are the more gracile morphotype, and one juvenile that cannot be assigned to either morphotype because the skull anterior to the nares is missing. This is the first clear evidence of sexual dimorphism in phytosaurs, and has important implications for phytosaur species-level taxonomy.

Keywords: phytosaurs, sexual dimorphism, pseudopalatine, Norian, Petrified Forest Formation, Chinle

INTRODUCTION

The Canjilon quarry, first excavated by Charles Camp for the University of California Museum of Paleontology (UCMP) in 1928 and 1933, is located just north and west of Ghost Ranch in north-central New Mexico (Fig. 1A) (Hunt and Lucas, 1989; Long et al., 1989). After Camp's excavations, both Harvard and Ghost Ranch excavated fossils at the Canjilon quarry. The quarry has yielded an enormous volume of phytosaur material, including at least 11 skulls in the UCMP collection and another in the Ghost Ranch collection. At least two individuals of the aetosaur *Typothorax coccinarum* have been found at the same stratigraphic level approximately 100 m from the quarry. The locality is stratigraphically high in the Petrified Forest Formation of the Upper Triassic Chinle Group and is approximately 90 m below the Jurassic Entrada Sandstone (Fig. 1B) (Lucas and Hunt, 1992; Hunt and Lucas, 1993). The presence of the aetosaur *Typothorax coccinarum* at the same stratigraphic level as the Canjilon quarry establishes a Revueltian (early-mid Norian) age for the quarry, an age assignment corroborated by the presence of *Pseudopalatus* (Lucas and Hunt, 1993; Lucas, 1998).

Phytosaur skulls from the Canjilon quarry were originally referred to *Rutiodon* (Gregory, 1962a,b; Lawler, 1974), and later (and we believe correctly) to *Pseudopalatus* (Ballew, 1985, 1989; Long and Murry, 1995). The sample of phytosaurs from the Canjilon quarry contains two very distinct skull morphotypes that may be attributed either to taxonomic differences at a generic or specific level (e.g., Ballew, 1985, 1989) or to the normal variation in a population of a single species. We propose that the two skull morph-otypes from the Canjilon quarry are sexual dimorphs and make that proposition here.

Institutional abbreviations: GR = Ruth Hall Museum of Paleontology, Ghost Ranch, Abiquiu, New Mexico; UCMP = University of California Museum of Paleontology, Berkeley.

TAPHONOMY

Initial taphonomic evaluation of the Canjilon quarry reveals a mixture of articulated and disarticulated associated skeletal material (Fig. 2). There does not appear to be substantial fluvial transport of these fossils, based on the presence of at least two fully articulated phytosaur skeletons and numerous clusters of associated material. There is a minor degree of orientation to some of the long elements, but not enough to indicate significant transport by water. The sediments that contain these remains are bentonitic mudstones typical of floodplain deposits in the Chinle Group, and the occurrence of the bones in mudstone also suggests little or no postmortem transport of the fossils.

Taphonomically, the floodplain is typically host to attritional assemblages of largely disarticulated vertebrate remains, whereas pond and river sediments hold either thick accumulations of attritional remains or catastrophic assemblages (Behrensmeyer, 1982). However, the abundance of material found at the Canjilon quarry and the excellent preservation of the fossils do not support an interpretation of the quarry as an attritional assemblage. Thus, the quarry appears to most likely preserve a catastrophic mass death assemblage of phytosaurs and other tetrapods. As such, it is reasonable to infer that it represents a sample of a local population of these animals (Martin, 1999).

We are not the only ones to study the taphonomy of the Canjilon quarry. Hunt and Downs (2002) reached similar conclusions independent of our research.

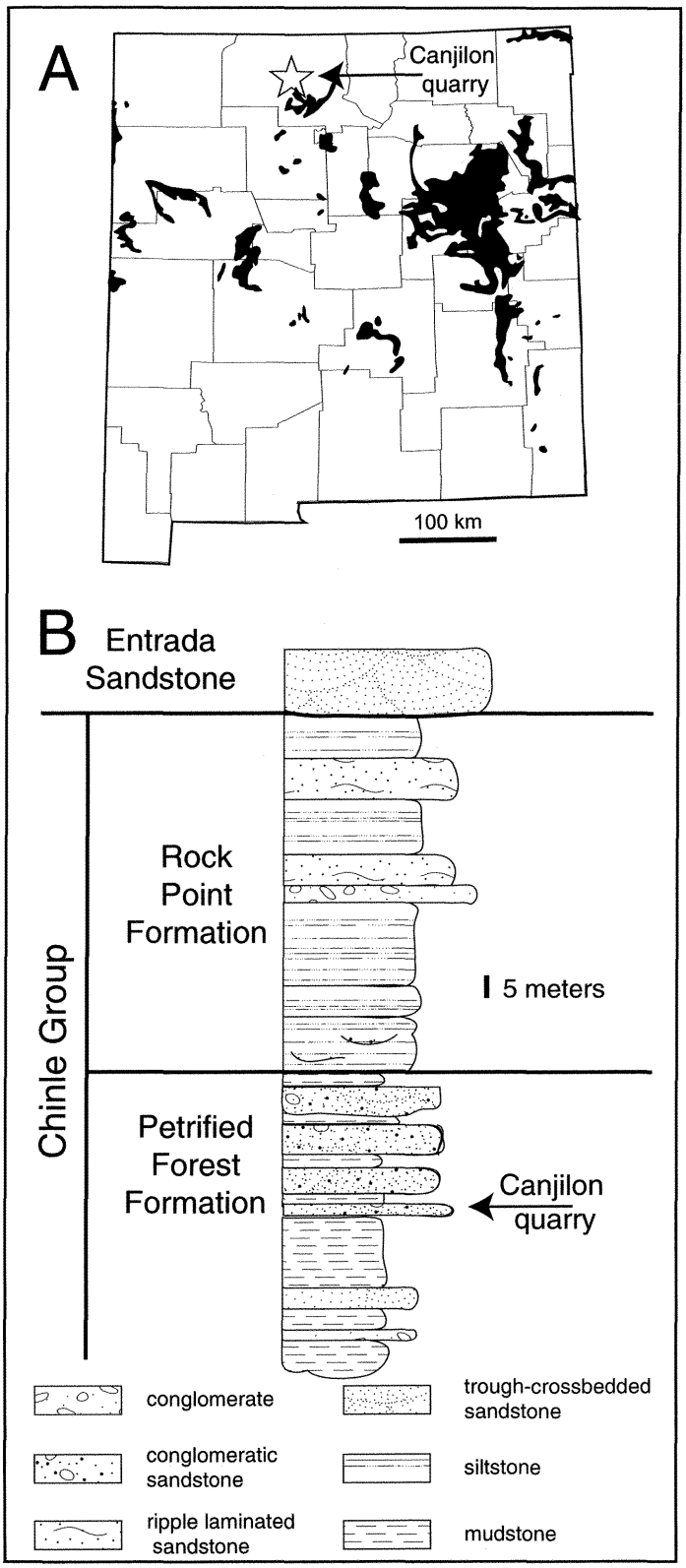

FIGURE 1. Geographic and stratigraphic position of the Canjilon quarry. **A**, Distribution of Triassic strata in New Mexico. Star denotes the location of the Canjilon quarry (UCMP V-2816). **B**, Stratigraphic column indicating the position of the Canjilon quarry (from Lucas and Hunt, 1992).

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Morphology

Of the 12 skulls recovered from the quarry,we re-examined 10 UCMP skulls and one Ghost Ranch skull. Both the general skull and specific bone dimensions were measured in all specimens (See appendix). Where visible, suture patterns were sketched, described and photographed. Even in a qualitative visual examination, two very distinct skull types are immediately evident (Figs. 3-6). Of the examined sample, six of the skulls have a very abrupt, distinct narial crest that can be described as volcano-like, as well as a very long and slender snout (Figs. 3A, B, C; 4A, B, C; 5A, B, C; 6B). Three of the skulls have very tall and comparatively robust narial crests and snouts (Figs. 3D, E; 4D, E; 5D; 6A). Three of the 12 skulls were not of use in this assessment for several reasons. One skull is missing its superior aspect, one (a juvenile) is missing the snout immediately anterior to the external nares, and the third was too damaged to be included.

All specimens examined have supratemporal fenestrae that are narrow and often slit-like in dorsal view, and they have u-shaped occipital complexes. The squamosals are moderately wide, and the suture positions, particularly in the posterior portion of the skull, are essentially identical among the different individuals. Comparison of suture positions and the measurements taken of the bones of the skull reveal that the only significant difference between the two variants is in the dimensions, and thus the relative proportions, of the premaxillae (Figs. 3-6, Table 1). The premaxillae are a pair of long, approximately rectangular bones that form the long snout. They are bordered posteriorly by the maxillae, the nasals and the septomaxillae (in ventral to dorsal order). In these two morphotypes, the premaxillae define the length and width of the narial crest. In the skull variant with the robust, tall narial crest, the premaxillae are taller and more robust than the premaxillae in the more gracile variant. Apparent variations in the dimensions of other bones and fenestrae are due to preservational distortion.

Interpretation

Traditionally, phytosaurian taxonomic assignments have been made based primarily on features of the dorsal portion of the skull (e.g., McGregor, 1906; Camp, 1930; Gregory, 1962a; Westphal, 1976; Ballew, 1989; Hunt, 1994; Long and Murry, 1995). Differences in the position and size of the supratemporal fenestrae as well as differences in the dimensions of the squamosal processes and occipital complex are considered key features for defining phytosaur taxa. In all of the Canjilon phytosaur skulls, the supratemporal fenestrae and squamosal processes are essentially identical. The dimensions and positions of the bones and

TABLE 1. Selected measurements (in mm) of Canjilon quarry phytosaur skulls with statistical analyses.

Catalogue number	Max. length	Snout length	Postsnout length	Max. width	Interorbit distance	Crest height	Crest length
Males							
UCMP34250	874	506	368	358	52	124	324
UCMP34246	1101	492	609	424	7	108	423
UCMP27228	922	595	327	363	57	212	241
Mean	**965.7**	**531.0**	**434.7**	**381.7**	**59.7**	**148.0**	**329.3**
Females							
UCMP27234	922	591	331	304	48	147	146
UCMP34245	1075	660	415	330	49	130	230
UCMP34249	890	542	348	293	43	105	168
UCMP27231	750	386	374	308	51	137	236
GR147	1036	667	369	280	47	139	113
Mean	**934.6**	**569.2**	**367.4**	**303**	**47.6**	**131.6**	**178.6**

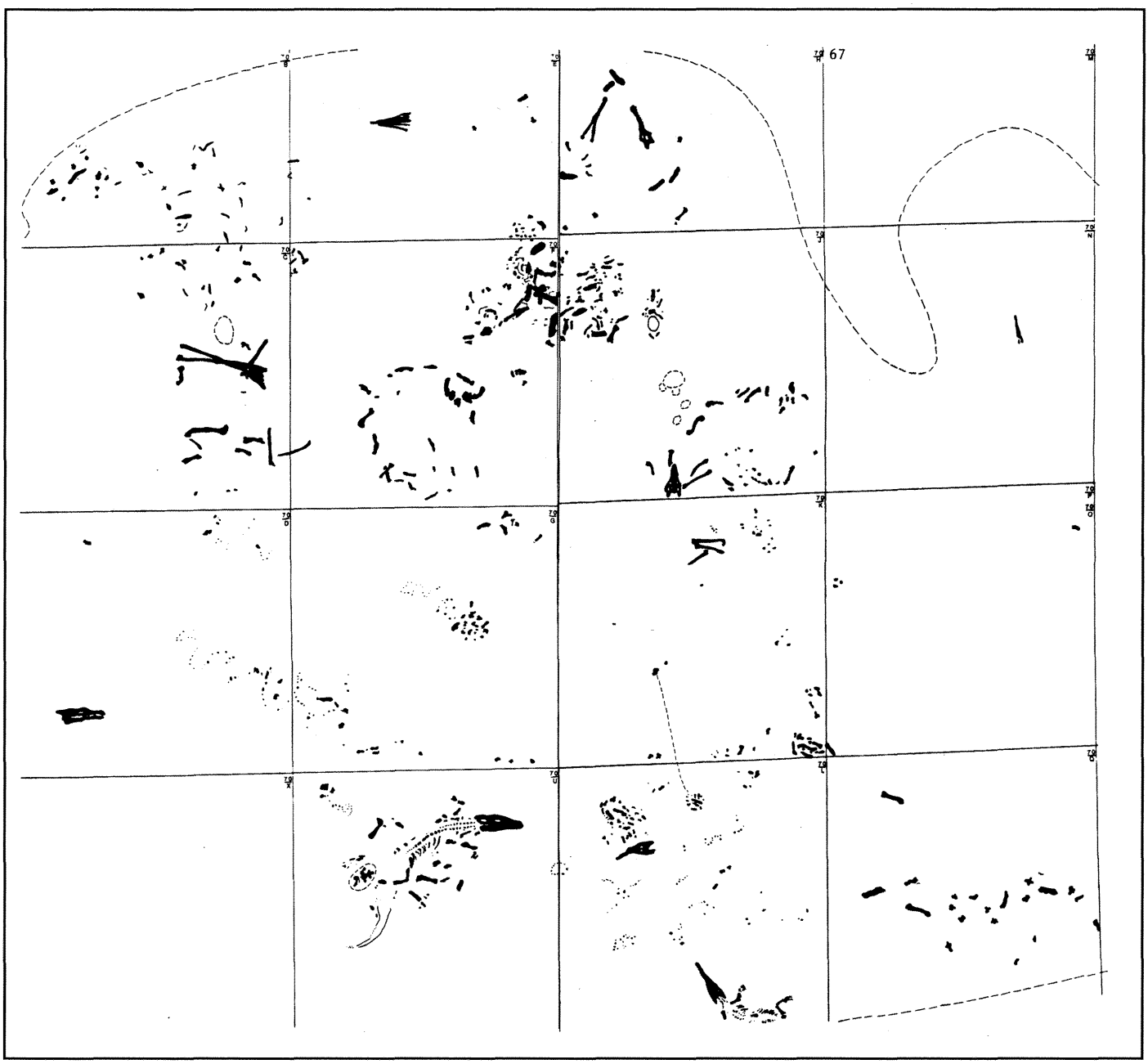

FIGURE 2. Map of part of the Canjilon phytosaur quarry. Each square is approximately 6x6 m (from Hunt and Lucas, 1993).

sutures of the skull deck do not vary significantly from specimen to specimen within the sample, and the ventral aspects of the skulls are all nearly identical.

Given that no features of the skull other than the narial crests vary significantly among the Canjilon phytosaur skulls, separation of the specimens into different taxa (Ballew, 1985) can only be based on the differences in narial crest morphology. However, given that there are two discrete morphotypes in this population sample of phytosaur skulls, a simple explanation is that they are two distinct variants within a single species, which is best explained by sexual dimorphism. The slender-snouted skulls with the small narial crest are most likely the females of the species, whereas the more robust skulls with the large crests are the male morph. In fact, it is likely that the tall narial crest is a display feature similar to those seen in some other tetrapods (see below).

Specimen Descriptions

UCMP 34250 is the best preserved of the three "male" skulls (Fig. 3D, 4D, 5D. 6A). The skull is 874 mm long from the tip of the snout to the posterior edge of the squamosal process and is 358 mm wide across the quadrates. The narial crest is 124 mm high and 324 mm long and is elevated above the skull deck (though this may be in part an artifact of post-mortem crushing).

UCMP 34246 is a very large specimen of the male morphotype (Fig. 3E, 4E). The skull is 1101 mm long from the anterior tip of the snout to the posterior edge of the squamosal processes. The specimen is 424 mm wide across the quadrates. The narial crest is 108 mm high and 423 mm long, and is elevated just above the skull deck. This specimen is strongly laterally compressed by post-mortem stresses, and the snout is broken at the

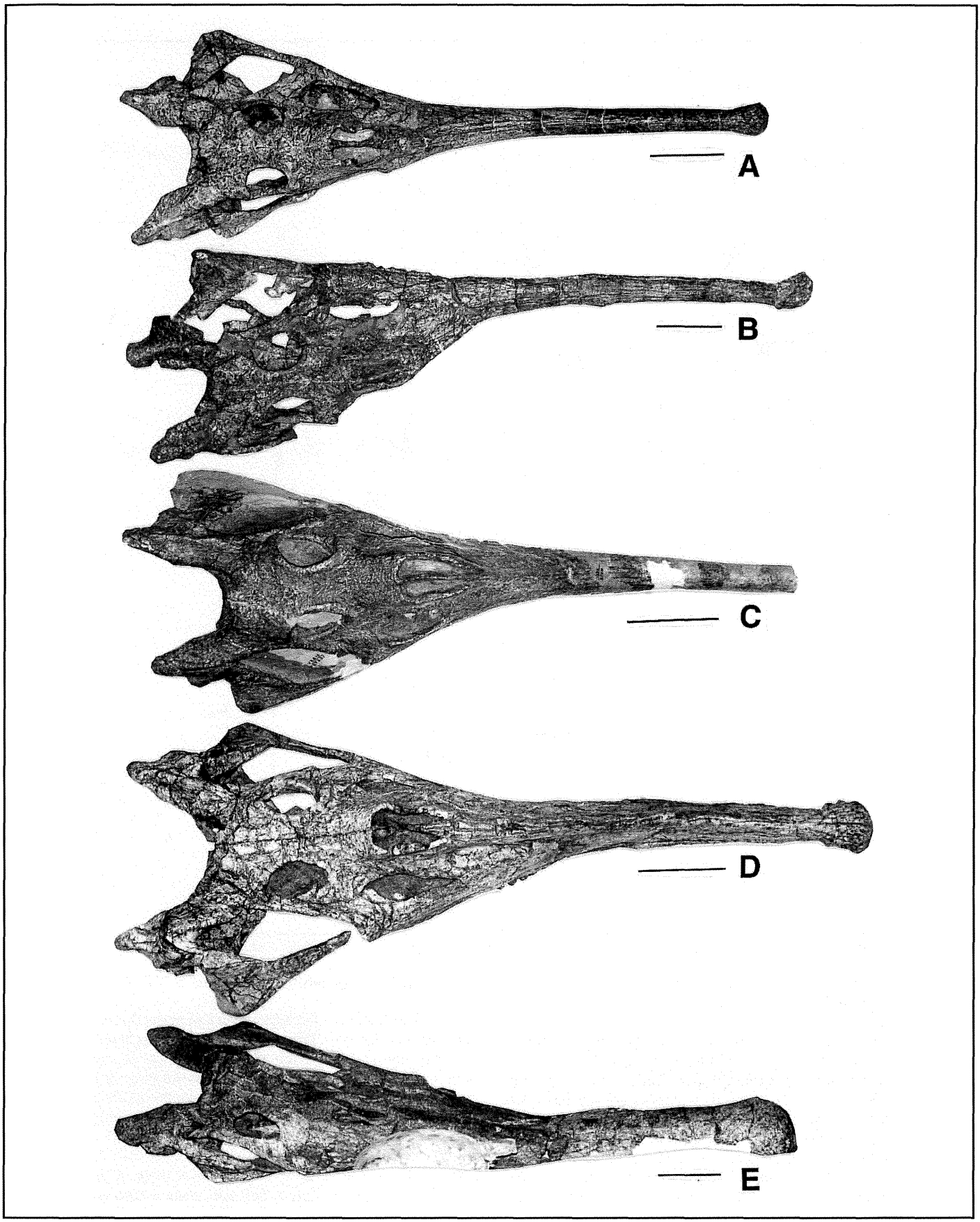

FIGURE 3. Dorsal views of sexual dimorphs of *Pseudopalatus* from the Canjilon quarry. Female morphotypes: **A**, UCMP 34249, **B**, UCMP 34245, **C**, UCMP 27231. Male morphotypes: **D**, UCMP 34250, **E**, UCMP 34246. Scale bar = 10 cm.

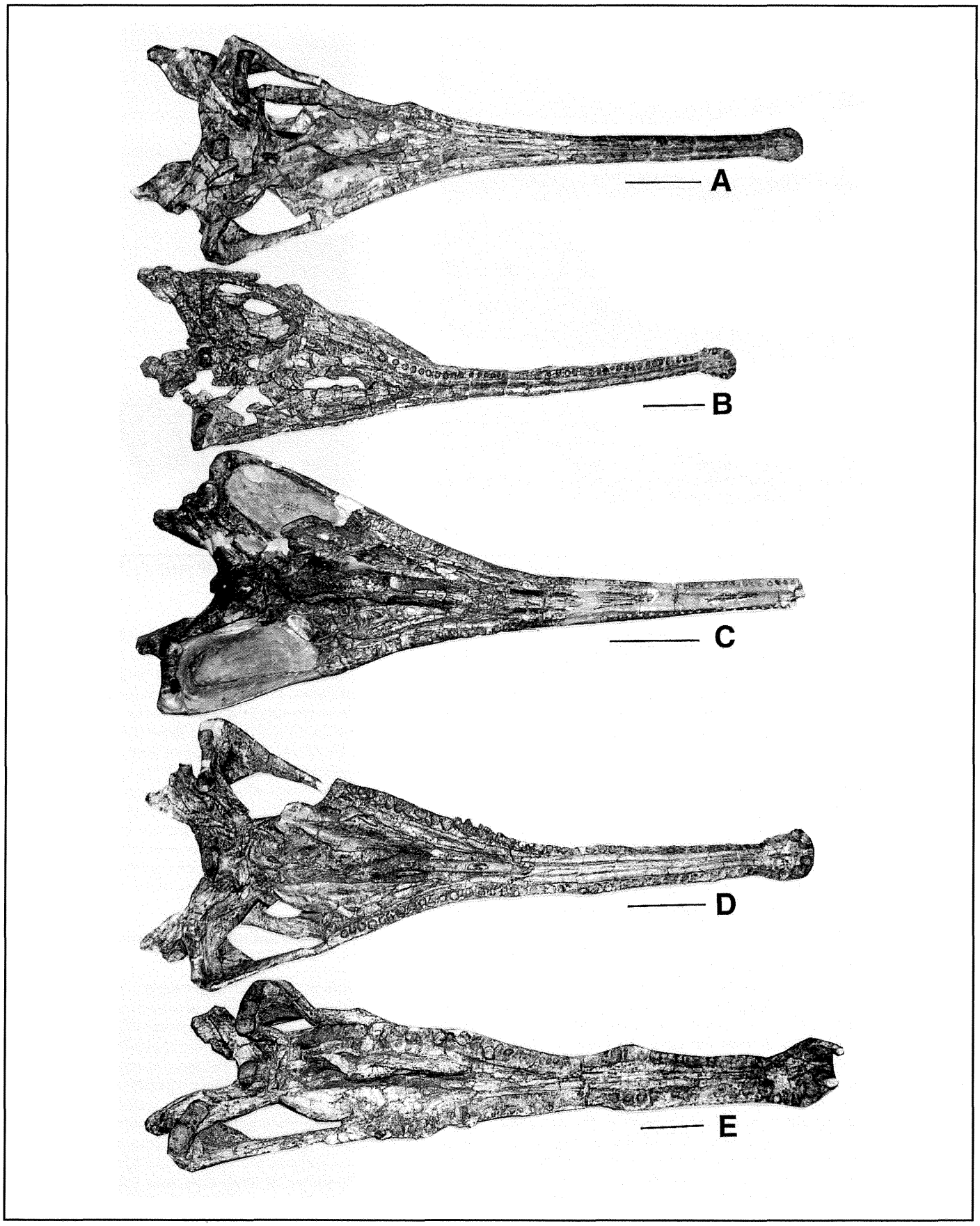

FIGURE 4. Ventral views of sexual dimorphs from the Canjilon quarry. Female morphotypes: **A**, UCMP 34249, **B**, UCMP 34245, **C**, UCMP 27231. Male morphotypes: **D**, UCMP 34250, **E**, UCMP 34246. Scale bar = 10 cm.

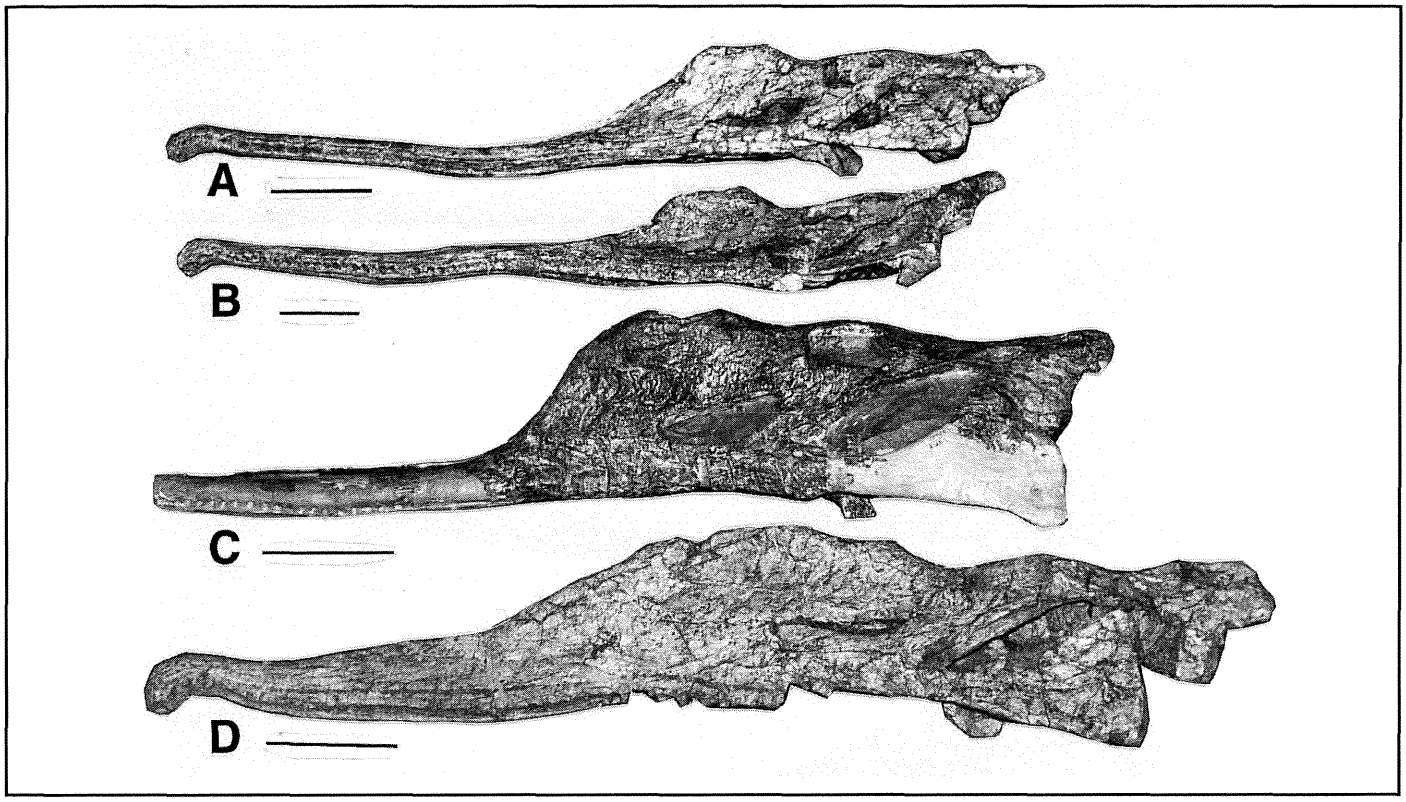

FIGURE 5. Lateral view of sexual dimorphs from the Canjilon quarry. Female morphotypes: **A**, UCMP 34249, **B**, UCMP 34245, **C**, UCMP 27231. Male morphotype: **D**, UCMP 34250. Scale bar = 10 cm.

anterior edge of the rostral crest.

UCMP 27228 is a third example of the "male" morphotype. This skull is 922 mm long from snout to squamosals and is 363 mm wide across the quadrates. The narial crest is 212 mm high and 241 mm long and is elevated above the skull deck. This specimen is also laterally compressed, which exaggerates the height of the narial crest, and has sustained severe damage to the right side of the skull.

UCMP 34249 is the best preserved example of the female morphotype (Fig. 3A, 4A, 5A, 6B). This skull is 890 mm long and 293 mm wide across the quadrates. The narial crest is 105 mm high and 168 mm long. It is elevated above the level of the skull deck. We note that the crest of this skull is both relatively and absolutely smaller than the crest of the slightly shorter male skull. This demonstrates that crest size does not solely correlate to the size of the skull itself.

UCMP 34245 is also a female morphotype skull (Fig. 3B, 4B, 5B). This skull is 1075 mm long from the snout to the squamosals and 330 mm across the quadrates. The narial crest is 130 mm high and 230 mm long and is elevated above the skull deck. The right side of this specimen has been crushed.

There are at least three more female morphotype skulls in the UCMP collections. UCMP 27231 is a female skull that is at minimum 750 mm long (anterior half of the snout is missing) and 308 mm wide (Fig. 3C, 4C, 5C). The narial crest is 137 mm high and 236 mm long. Another skull, UCMP 27234 is 922 mm long and 304 mm wide. The narial crest is 147 mm high (though it has been partially reconstructed) and 146 mm long. Most of the crest area has been heavily reconstructed on this specimen. UCMP 34251 is another female skull that lacks the rostrum immediately anterior to the narial crest. This skull is 102 mm wide and the narial crest is 225 mm high and 276 mm long.

The final specimen of the female morphotype, GR 147, was excavated in the summer of 2001 and is only partially prepared. The skull is 1036 mm long, and the width was not determined. The narial crest is 139 mm high and 113 mm long.

In the sample represented by the death assemblage at the Canjilon quarry, there are six of the female variant (UCMP 34249, 34245, 27231, 27234, 34251, GR 147) and three of the male variant (UCMP 34250, 34246, 27228). Of the male variants, two of the three specimens are subadults (UCMP 34250, 27228), whereas the third (UCMP 34246) is a very large adult and the largest of the Canjilon skulls. The relative proportion of females to males in this population conforms with the proportions of the two sexes seen in gregarious polygynous animal populations: several females and one or two adult males, which conforms with current theories on polygyny and sexual dimorphism (Jungers, 1985; Andersson, 1994 and references therein).

Variation and Sexual Dimorphism in Fossil and Modern Tetrapods

Analogies with modern tetrapods suggest that the two rostral crest morphotypes of the Canjilon phytosaurs are an example of sexual dimorphism. In most modern groups of amphibians and reptiles, sexually dimorphic features are typically in the soft tissue and thus will not preserve in the fossil record (Olson, 1968). There are, however, some features that do preserve and have been deemed as dimorphic characters by previous authors. Davitaschvili (1961) identified as possibly sexually dimorphic features the long neural spines of some pelycosaurs, horns in the theropod dinosaur *Ceratosaurus*, the crests of hadrosaurs (see also Dodson, 1975), the plates of stegosaurs, and frills and horns of ceratopsians (also see Farlow and Dodson, 1975; Dodson, 1976). Olson (1968) argued that if a dimorphic character appears in samples that otherwise seem to have all the characteristics of a single species, then this character most likely represents sexual

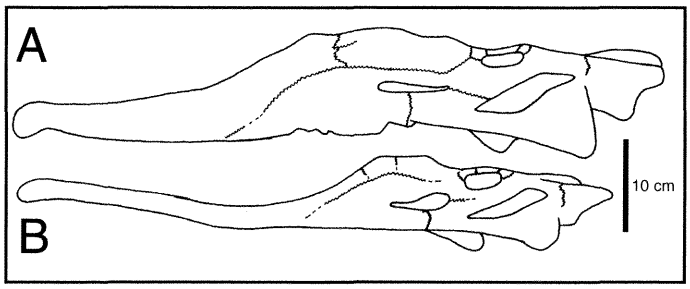

FIGURE 6. Sexual dimorphs of the phytosaur *Pseudopalatus* from the Canjilon quarry. **A**, Line drawing of 34250 (male) in left lateral view; **B**, Line drawing of 34249 (female) in left lateral view. Scale bar = 10 cm.

dimorphism. However, it is very difficult to judge whether or not a sample is dimorphic if the sample size is small, because the total range of natural variation in that population is not known (Olson, 1968).

In the ceratopsian dinosaur *Protoceratops*, there are two variants in a single sample, with frill length increasing with the size of the skull and probably serving as a visual dominance display feature (Farlow and Dodson, 1975; Dodson, 1976; Tereschenko, 2001). Ceratopsians with long frills (*Chasmosaurus, Anchiceratops, Pentaceratops, Arhinoceratops* and *Torosaurus*) present a prominent frontal display of the frill and horns when the head is inclined forward (Farlow and Dodson, 1975).

There is evidence of moderate sexual dimorphism in modern crocodile populations. Modern crocodilians are the closest living relatives of phytosaurs (e.g., Benton and Clark, 1988) and are also the closest modern analogue to phytosaurs (Hunt, 1989); thus, the sexual dimorphism and related behavior in crocodilians can be appropriately compared to phytosaur dimorphism. In surveys of the Australian estuary crocodile, *Crocodylus porosus*, males tend to have longer tails (though there is a limited statistical difference) (Webb and Messel, 1978). Females show a marked expansion of the central portion of the skull through widening of the interocular region and the cranial midpoint width. Webb and Messel (1978) suggest that there is some evidence that sexual dimorphism in crocodiles increases with body size, with males being 25% larger than females. Neill (1971) has observed that crocodilians appear to be more impressed by a strongly vertical display structure versus a horizontal structure.

Modern ungulates and lizards provide a more distinct example of sexual dimorphism. Over time, there has been a trend towards an increase in cephalization of the display structures (horns) of modern ungulates such as *Bos* and *Bison* (Geist, 1966). Some lizards have paralleled this trend with a development of horn-like soft tissue structures on the head that are used for display (Farlow and Dodson, 1975).

What this survey demonstrates is that fossilizable structures that are sexually dimorphic typically are cranial structures used for (or interpreted as for) visual display. The dimorphic narial crests of the Canjilon quarry phytosaurs fit this pattern of a male with a hypertrophied cranial structure used for visual display. Therefore, the evidence of sexual dimorphism in these modern and fossil groups, especially lizards, crocodilians and other archosaurs, is consistent with our interpretation that the Canjilon quarry phytosaurs represent a sexually dimorphic population.

Ecological Variants

Hunt (1989, 1994) explained much of the morphological variation in phytosaur crania by positing the existence of three ecological variants. Thus, gracile skulls (dolichorostral) represent aquatic species, robust skulls (brachyrostral) represent terrestrial species, and skulls of intermediate proportions (altirostral) are semi-aquatic animals (Hunt, 1994). Based on the sexual dimorphism evident in the Canjilon quarry sample, we propose that there may be, in fact, two variants that are sexually dimorphic within any phytosaur species. Thus, we would redistribute Hunt's three ecological variants. The gracile or dolichorostral skulls represent the females of species A. Intermediate morphology skulls (altirostral) include males of species A and females of a generally more robust species B, and the posterior portions of the skulls must be carefully examined to separate them into their respective taxa. The robust individuals (brachyrostral) are the males of species B. We agree with Hunt (1989, 1994) that the ecological significance of these skull variations is that species A, the more gracile group, was aquatic or semi-aquatic, whereas the robust species B was more terrestrial. There is some geologic evidence to support this niche partitioning. Regardless of the taxonomic scheme used, it is evident that dolichorostral skulls are more common in the rock record than brachyrostral skulls (Hunt, 1994; Long and Murry, 1995). Dolichorostral skulls, typically thought to be associated with piscivory (Hunt, 1989), are often found in fluvial deposits and other environments suggesting aquatic habitats. Brachyrostral skulls are less common generally, and at least some, such as the holotype of *Smilosuchus* (=*Machaeroprosopus*) *gregorii* Camp from the Blue Hills of Arizona, were recovered from pedogenically modified strata that probably represent distal floodplain deposits (Camp, 1930; personal observations). Clearly, further work is needed, including a more detailed study of the alpha taxonomy and a concerted effort to evaluate the taphonomy of known phytosaur localities in a more modern context. Still, detailed examination of the geological context of phytosaur occurrences provides a means to test the hypotheses we advance here as well as the paleoecological hypotheses of Hunt (1989, 1994).

CONCLUSIONS

There are two possibilities to explain the cranial variation in the Canjilon quarry phytosaur sample. The first is that there were two taxa living in close proximity within the fluvial/floodplain ecosystem. In this scenario, the robust skulls represent the more terrestrial species or genus, whereas the gracile skulls represent a more aquatic taxon. The other possibility is that the phytosaurs from the quarry represent two morphotypes of a single species. Because the mass death assemblage found at the Canjilon quarry most likely represents a single population sample of phytosaurs, it is unlikely that the variation seen in the skulls is taxonomic, especially given that the skulls are essentially identical in all morphological details except for the narial crests. The most parsimonious explanation of this variation is sexual dimorphism. The individuals with the expanded narial crests are the males, whereas those with the abrupt, volcano-like nares are the females of the population.

Thus, the Canjilon phytosaur sample represents the first strong evidence of sexual dimorphism in phytosaurs. We believe that re-evaluation of other phytosaur genera and species will reveal a similar pattern of variation. Most phytosaurian taxa have been given separate generic or specific names based on differences in skull morphology. It is important to recognize that there was significant biological variation in a phytosaur population, and that some of it may have had its origin in sexual dimorphism.

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APPENDIX—MEASUREMENTS AND CHARACTERISTICS OF CANJILON QUARRY PHYTOSAUR SKULLS

Skull ID	**UCMP 27228**	**UCMP 27231**	**UCMP 27234**	**UCMP 34228**	**UCMP 34245**
Gender	male	female	female	not known	female
Skull length	922 mm	750 mm	922 mm	No rostrum	1075 mm
Maximum width	363 mm	308 mm	304 mm	113 mm	330 mm
Snout length	595 mm	386 mm	591 mm	not present	660 mm
Post-snout length	327 mm	374 mm	331 mm	180 mm	415 mm
Max width snout	55 mm	54 mm	65 mm	not present	59 mm
Max height crest	212 mm	137 mm	147 mm	not present	130 mm
Max length crest	241 mm	236 mm	146 mm	not present	230 mm
Crest description	Robust	Volcano-like	Volcano-like	not present	Volcano-like
Crest position	above skull deck	above skull deck	reconstructed	not present	above skull deck
Squamosal width	56 mm	58 mm	reconstructed	28 mm	80 mm
Squamosal length	120 mm	91 mm	reconstructed	66 mm	118 mm
Intersquamosal width	180 mm	144 mm	reconstructed	63 mm	176 mm
Maxilla width	82 mm	4.9 mm	reconstructed	not present	94 mm
Maxilla length	321 mm	210 mm	reconstructed	not present	276 mm

Skull ID	UCMP 27228	UCMP 27231	UCMP 27234	UCMP 34228	UCMP 34245
Nasal width	65 mm	32 mm	reconstructed	16 mm	52 mm
Nasal length	226 mm	161 mm	reconstructed	not present	216 mm
Septomaxilla width	38 mm	15 mm	reconstructed	not present	36 mm
Septomaxilla length	112 mm	60 mm	reconstructed	not present	61 mm
Premaxilla width	36 mm	54 mm	reconstructed	not present	59 mm
Premaxilla length	409 mm	227 mm	reconstructed	not present	487 mm
Nares width	31 mm	16 mm	reconstructed	13 mm	20 mm
Nares length	68	62 mm	reconstructed	not present	79 mm
Skull deck height	n.m.	144 mm	153 mm	82 mm	133 mm
Supratmp. fen. width	16 mm	8 mm	reconstructed	7 mm	13 mm
Supratmp. fen. length	64 mm	47 mm	reconstructed	15 mm	41 mm
Interfen. width	n.m. (right side n.p.)	38 mm	reconstructed	28 mm	60 mm
Lat. temp. fen. width	91 mm	64 mm	reconstructed	32 mm	80 mm
Lat. temp. fen. length	228 mm	148 mm	reconstructed	75 mm	224 mm
Interfen. width	n.m.	136 mm	reconstructed	65 mm	160 mm
Antorb. fen. width	68 mm	40 mm	reconstructed	n.m.	42 mm
Antorb. fen. length	152 mm	94 mm	reconstructed	n.m.	106 mm
Interfen. width	n.m.	85 mm	reconstructed	n.m.	118 mm
Quad.ju. width	115 mm	105 mm	reconstructed	31 mm	95 mm
Quad.ju. length	194 mm	127 mm	reconstructed	67 mm	123 mm
Jugal width	43 mm	30 mm	reconstructed	13 mm	27 mm
Jugal length	184 mm	127 mm	reconstructed	117 mm	147 mm
Lachrymal width	74 mm	45 mm	reconstructed	12 mm	58 mm
Lachrymal length	136 mm	151 mm	reconstructed	52 mm	182 mm
Parietal width	107 mm	27 mm	reconstructed	37 mm	33 mm
Parietal length	59 mm	52 mm	reconstructed	35 mm	66 mm
Postfrontal width	31 mm	34 mm	reconstructed	12 mm	37 mm
Postfrontal length	43 mm	31 mm	reconstructed	19 mm	25 mm
Prefrontal width	28 mm	25 mm	reconstructed	n.m.	12 mm
Prefrontal length	36 mm	21 mm	reconstructed	n.m.	33 mm
Frontal width	36 mm	25 mm	reconstructed	13 mm	25 mm
Frontal length	107 mm	82 mm	reconstructed	50 mm	79 mm
Orbit width	68 mm	65 mm	72 mm	30 mm	56 mm
Orbit length	88 mm	45 mm	48 mm	35 mm	78 mm
Min. interorb. length	57 mm	51 mm	reconstructed	n.m.	49 mm
Quadrate width	25 mm	19 mm	reconstructed	36 mm	87 mm
Quadrate length	105 mm	80 mm	reconstructed	11 mm	19 mm
Interquad. length	not measured	225 mm	reconstructed	76 mm	227 mm
Palate width	45 mm	151 mm	reconstructed	n.m.	34 mm
Palate length	201 mm	27 mm	reconstructed	n.m.	195 mm
Pterygoid width	not present	45 mm	reconstructed	n.m.	51 mm
Pterygoid length	not present	74 mm	reconstructed	n.m.	96 mm
Pterygoid flange span	not present	118 mm	reconstructed	n.m.	82 mm
Ectopterygoid width	19 mm	23 mm	reconstructed	n.m.	n.m.
Ectopterygoid length	55 mm	42 mm	reconstructed	n.m.	n.m.
Basioccipital width	61 mm	65 mm	reconstructed	32 mm	77 mm
Occipital length	67 mm	62 mm	reconstructed	32 mm	59 mm
Occ. condyle width	47 mm	38 mm	reconstructed	19 mm	41 mm

Skull ID	UCMP 34246	UCMP 34249	UCMP 34250	UCMP 34251	GR 147
Gender	male	female	male	female	unprepped female
Skull length	1101 mm	890 mm	874 mm	No rostrum	1036 mm
Maximum width	424 mm	293 mm	358 mm	102 mm	280 mm
Snout length	492 mm	542 mm	506 mm	not present	667 mm
Post-snout length	609 mm	348 mm	368 mm	409 mm	369 mm
Max width snout	112 mm	47 mm	60 mm	not present	58 mm
Max height crest	108 mm	105 mm	124 mm	225 mm	139 mm
Max length crest	423 mm	168 mm	324 mm	276 mm	113 mm
Crest description	Robust	Volcano-like	Robust,	Volc.-like(distorted)	Volcano-like
Crest position	above skull deck	above skull deck	above skull deck	above skull deck	above skull deck
Squamosal width	66 mm	68 mm	73 mm	57 mm	63 mm
Squamosal length	126 mm	96 mm	162 mm	114 mm	94 mm

Skull ID	UCMP 34246	UCMP 34249	UCMP 34250	UCMP 34251	GR 147
Intersquamosal width	226 mm	169 mm	195 mm	118 mm	121 mm
Maxilla width	45 mm	51 mm	40 mm	35 mm	51 mm
Maxilla length	420mm	245 mm	235 mm	272 mm	256 mm
Nasal width	43 mm	36 mm	45 mm	n.m.	40 mm
Nasal length	307 mm	140 mm	141 mm	n.m.	145 mm
Septomaxilla width	43 mm	28 mm	40 mm	n.m.	21 mm
Septomaxilla length	95 mm	30 mm	133 mm	n.m.	83 mm
Premaxilla width	112 mm	47 mm	31 mm	n.m.	28 mm
Premaxilla length	413 mm	450 mm	423 mm	n.m.	593 mm
Nares width	23 mm	15 mm	24 mm	18 mm	18 mm
Nares length	90 mm	62 mm	75 mm	75 mm	58 mm
Skull deck height	201 mm	65 mm	125 mm	159 mm	n.m.
Supratmp. fen. width	25 mm	12 mm	11 mm	11 mm	10 mm
Supratmp. fen. length	41 mm	33 mm	45 mm	33 mm	32 mm
Interfen. width	90 mm	52 mm	41 mm	49 mm	56 mm
Lat. temp. fen. width	86 mm	64 mm	62 mm	84 mm	62 mm
Lat. temp. fen. length	231 mm	149 mm	171 mm	196 mm	146 mm
Interfen. width	163 mm	139 mm	155 mm	111 mm	152 mm
Antorb. fen. width	46 mm	36 mm	27 mm	45 mm	32 mm
Antorb. fen. length	162 mm	106 mm	95 mm	114 mm	93 mm
Interfen. width	n.m. (right crushed)	94 mm	89 mm	60 mm	101 mm
Quad.ju. width	133 mm	74 mm	88 mm	97 mm	69 mm
Quad.ju. length	175 mm	108 mm	110 mm	129 mm	91 mm
Jugal width	49 mm	27 mm	43 mm	40 mm	24 mm
Jugal length	116 mm	100 mm	146 mm	128 mm	100 mm
Lachrymal width	58 mm	39 mm	44 mm	49 mm	45 mm
Lachrymal length	158 mm	123 mm	118 mm	154 mm	85 mm
Parietal width	40 mm	28 mm	78 mm	30 mm	28 mm
Parietal length	73 mm	58 mm	26 mm	61 mm	45 mm
Postfrontal width	34 mm	28 mm	29 mm	37 mm	29 mm
Postfrontal length	38 mm	26 mm	28 mm	29 mm	26 mm
Prefrontal width	51 mm	n.m.	46 mm	n.m.	22 mm
Prefrontal length	43 mm	n.m.	30 mm	n.m.	18 mm
Frontal width	32 mm	21 mm	25 mm	28 mm	23 mm
Frontal length	101 mm	67 mm	103 mm	83 mm	88 mm
Orbit width	47 mm	49 mm	47 mm	62 mm	47 mm
Orbit length	80 mm	56 mm	69 mm	67 mm	57 mm
Min. interorb. length	70 mm	43 mm	52 mm	54 mm	47 mm
Quadrate width	107 mm	68 mm	95 mm	82 mm	not measured
Quadrate length	34 mm	15 mm	27 mm	17 mm	not measured
Interquad. length	252 mm	211 mm	204 mm	159 mm	not measured
Palate width	39 mm	31 mm	44 mm	28 mm	not measured
Palate length	242 mm	151 mm	179 mm	198 mm	not measured
Pterygoid width	80 mm	49 mm	46 mm	51 mm	not measured
Pterygoid length	109 mm	51 mm	89 mm	92 mm	not measured
Pterygoid flange span	97 mm	88 mm	90 mm	66 mm	not measured
Ectopterygoid width	30 mm	n.p.	21 mm	10 mm	not measured
Ectopterygoid length	76 mm	n.p.	35 mm	43 mm	not measured
Basioccipital width	95 mm	65 mm	75 mm	68 mm	not measured
Occipital length	82 mm	66 mm	55 mm	64 mm	not measured
Occ. condyle width	45 mm	37 mm	40 mm	37 mm	not measured